Scaling and the Effects of Plant, Soil, and Landscape Characteristics on Sap-Feeding Herbivores in Cotton

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ABSTRACT Soil physical and chemical properties can affect plant growth and nutrition, which in turn can affect a plant's attractiveness and susceptibility to insect herbivores. A further source of variation in these relationships is the spatial scale at which patterns are measured. Both the size of the area being sampled, or scale, and the distance between measurements, or grain, are parameters that affect interpretation of insect abundance patterns. Our objectives in this study were to determine both the relationship of various landscape, plant, and soil characteristics to densities of sap-feeding insect herbivores in cotton and to determine the effects of sampling scale and sampling grain on these relationships. We included three sap-feeding herbivores in our study: *Aphis gossypii* Glover, *Frankliniella occidentalis* (Pergande), and *Bemisia tabaci* Gennadius. We found that abundance of each insect species was related to several single factors within the cotton field and that these relationships were always dependent on the scale and grain of the measurements. No one variable or set of variables was related to a particular insect density for each scale and grain examined. However, some variables were significantly correlated with insect densities at the larger scale (622 by 31 m), although none were significantly correlated for all plots at the smaller scale (154 by 31 m). In comparing the separate effects of each variable using partial correlations, elevation was negatively correlated with *A. gossypii* density at both grains (samples taken 25 m apart and samples taken 50 m apart), whereas in multiple regression analyses including all variables, plant moisture and soil nitrates were positively correlated and plant height and clay negatively correlated with *A. gossypii* density. In examining the separate effect of each variable on *F. occidentalis* density, plant moisture was negatively associated with *F. occidentalis* density at each grain. In multiple regression analyses, no variable was associated with *F. occidentalis* density at each grain. For *B. tabaci*, soil salinity was positively associated when variables were examined separately or in multiple regression. We discuss the possible reasons for why particular variables are related to the densities of each species.

KEY WORDS plant nutrients, grain, aphid, thrips, whitefly

PLANT AND SOIL CHARACTERISTICS can have varying effects on herbivore densities (Wolfson 1980, Scriber 1984, Dale 1988). The main environmental factors that affect plant-to-plant variation within a single field are physical, chemical, and moisture variations in the soil (Treshow 1970, White 1984, Chapin 1991). Other factors that can affect plants and their herbivores, such as pollution, temperature, and pesticides, are more evenly distributed throughout a single field and have less effect on plant-to-plant variations (Alstad et al. 1982). Physical and chemical variations in soil that can affect plants include soil texture and depth, pH, salinity, and available nutrient levels, nitrogen in particular (Joyce 1958, McClure 1977, Clark 1982, Munns et al. 1982, White 1984). Plant growth is highly dependent on soil physical and chemical properties, and these factors affect patterns of insect herbivore abundance through changes in available nutrients (Mattson and Addy 1975, Tabashnik 1982, Dale 1988). Host-plant nutrition can also modify a plant's reaction to insects and its susceptibility to their feeding, creating conditions more or less favorable to insects (van Emden et al. 1969, Sharma 1970, Carrow and Betts 1973, Smirnoff and Bernier 1973, Mitchell and Paul 1974, Rhoades 1979, White 1984, Dale 1988).

Changes in the soil can affect plant hosts, which in turn can affect the herbivores that feed on them (Wolfson 1980, Clark 1982, Dale 1988, Funderburk et al. 1994). Among the causes of these variations are soil, plant, and insect factors (Rhoades 1979, White 1984, Dale 1988, Lambert and Heatherley 1991, Funderburk et al. 1994, Faria and Fernandes 2001, Hodkinson et al. 2001). Also, although less well documented, variation

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can occur because of differences in landscape structure such as elevation, slope, or soil depth (White 1984, Halvorson and Doll 1991, Qi and Wu 1996, Timlin et al. 1998). A further source of variation or a complicating factor in understanding these relationships is the spatial scale at which the different patterns are measured (Obeysekera and Rutchey 1997, Oline and Grant 2002). Both the size of the area being sampled and the distance between measurements, or grain, are scale parameters that can affect the interpretation of patterns of plant, soil, landscape, and insect characteristics (Bian and Walsh 1993, Rodriguez-Iturbe et al. 1995, Kotilar 1996, Brosofske et al. 1999, Western and Bloschl 1999, Oline and Grant 2002). Plant and soil variables are scale dependent, and consequently, their effects on insect distributions should be scale dependent. However, there is no published information on this topic.

Intraspecific variation in plants can exert strong selection pressure in herbivores, and whereas many studies have focused on plant–herbivore interactions, few have focused on the soil or landscape characters that affect herbivore choice (Wolfson 1980, Lambert and Heatherley 1991, Funderburk et al. 1994, Qi and Wu 1996). Plants usually contain lower concentrations of nutrients, in particular, proteins and amino acids, than insects need (Southwood 1972, McNeill and Southwood 1978). Some insects vary feeding sites on hosts (McNeill 1971) or switch hosts with changing plant nitrogen concentrations (McNeill and Southwood 1978). Plant choice is often made first by the mother during oviposition, although immatures of some species may make further choices between staying where they are at, moving on the plant, or moving to a different plant. Both Dethier (1959) and Chew (1977) believed that strong selection pressure against indiscriminate oviposition caused females to be selective in their choices, although mistakes can and do occur.

In agriculture, sound pest management strategies generally include the assessment of pest densities (Pedigo 1989). With this purpose and cost effectiveness in mind, sampling is done while averaging pest densities over large areas. One way to decrease the need for sampling insects throughout the season is to find plant or soil characteristics that can be used as predictors of insect densities. If these variables could be used to predict insect outbreaks, costs could be reduced by reducing sampling, and inputs, such as insecticides, by concentrating on problem areas (Yu et al. 2000). However, for any variable to be useful in predicting insect outbreaks, knowledge of the effects of sampling scale on these interactions is essential.

Although there are many studies on the effects of plant characteristics on herbivorous insects and a few studies on the effects of scale and grain on these relationships, to date we could find no studies that examine the effects of scale or grain on the relationship between landscape, plant, and soil characteristics and herbivore distributions. Our objectives in this study were to determine the relationship of various landscape, plant, and soil characteristics to densities of sap-feeding insect herbivores in cotton and to determine the effects of sampling scale and sampling grain on these relationships. We included three sap-feeding herbivores in our study: cotton aphid, *Aphis gossypii* Glover; western flower thrips, *Frankliniella occidentalis* (Pergande); and sweetpotato whitefly, *Bemisia tabaci* (Gennadius).

Materials and Methods

An experiment to determine the effects of landscape, plant, and soil characteristics and predators on densities of the sap-feeding insects, *A, gossypii, F. occidentalis,* and *B. tabaci* on cotton was carried out in 1998 at the Lamesa Agricultural Research farm of Texas A&M University on the Southern High Plains of Texas. Cotton variety 'Paymaster Roundup Ready 2326' was planted at a rate of 16.8 kg/ha on 8 May 1998. The site's soil, classified as Amarillo sandy loam, is well drained, highly erodible, and characterized by low electrical conductivity, moderate water holding capacity, mildly alkaline pH, and low organic matter content (Li et al. 2002).

To increase variability within the field, experimental treatments included low and high irrigation levels (50 and 75% potential evapotranspiration) applied through a low energy precision application (LEPA) pivot system to alternate furrows (Lascano 2000) and three nitrogen fertilizer levels (0, 90, and 135 kg/ha). The main field plot consisted of 32 rows of cotton in an ≈624-m-long arc, with the inner 16 rows irrigated at the low level and the outer 16 rows at the high level. The 32-row-wide, 622-m arc was divided into four, ≈154-m-long, blocks each separated by 2-m gaps. Each block was divided into three 50-m fertilizer plots with 2-m gaps between and the three fertilizer levels randomly applied one to each plot. Each fertilizer plot was further subdivided into four subplots within each irrigation plot for sampling (each 25 m long by 16 rows wide). This made for a total of 96 subplots sampled per week for the whole field, 24 for each block.

The low irrigation level was 50% of the annual evapotranspiration (ET) or ≈840 mm during the growing season (20 mm every 3 d). The high irrigation level was 75% ET or ≈1,200 mm during the growing season (20 mm every 3 d). These water inputs included three preplant applications of 57 mm for the whole field. Nitrogen fertilizer was applied using a 32-0-0 urea. For all three nitrogen levels, 45 kg/ha was applied at 5 d after plant emergence. Additionally, for the medium and high nitrogen levels, 45 kg/ha was applied 35 d after emergence, with an additional 45 ha added at the high nitrogen level 70 d after emergence.

Counts of nymphs of the sap-sucking herbivores *A. gossypii, F. occidentalis,* and *B. tabaci* and all predators on leaves were taken once per week during a 14-wk period beginning on 10 June and continuing through 9 September. Samples were taken by examining two leaves from each of two randomly selected plants from the center two rows of each treatment subplot (2 leaves/plant, 2 plants/subplot, 4 subplots/fertilizer plot, 3 fertilizer plots/replicate, 4 replicates/irrigation level, 2 irrigation levels = 384 leaves/wk). The two leaves examined were the first fully expanded leaf (the fifth or sixth node) and a leaf approximately halfway down the plant, with the latter progressing from node 7 in June to 10 in July, 13 in August, and ending with node 14 for the last sample in September. For each of the three herbivores, counts of nymphs were made on cotton leaves in the field. Predators sampled consisted mainly of spiders (not determined to species) and larvae of the two insect species, *Chrysoperla carnea* (Stephens) and *Hippodamia convergens* Guérin-Méneville. Two other predator species, insidious flower bug, *Orius insidiosus* (Say), and big-eyed bug, *Geocoris punctipes* (Say), were observed on plants, but because of their high mobility, were not included in counts of insects on leaves.

Soil samples for texture (proportions of sand, clay, and silt) and nitrate levels were taken once at the beginning of the experiment from a mixture of five composite soil samples within the center row of each subplot taken at 0-, 30-, 60-, and 90-cm depth (Li et al. 2001). Soil samples were air-dried and sieved to 2 mm for texture tests. Soil texture was measured using the hydrometer method (Gee and Bauder 1986). The 0.1 M KCL extractable soil nitrate was measured using a Technicon Auto-Analyzer II C (Technicon Instruments, Tarrytown, NY) (Li et al. 2001). Longitude, latitude, and elevation of sample areas were noted synchronously with soil samples using a global positioning system (GPS) unit. Soil electrical conductivity (salinity) and pH measurements were taken from the surface soil (0- to 30-cm depth) at the time of first irrigation, ≈8 wk after planting, and pH was measured every 21 d until harvest.

Plant height, moisture (Plant H_2O), and nitrogen content (NO^{-3}) were all measured once at the end of the season before harvest aids were applied. Measurements were taken by randomly selecting three plants from the center two rows of each subplot. To calculate moisture values, both wet and dry weights were taken on whole plants, and the proportion of wet weight minus dry weight to wet weight was calculated. Nitrogen content of whole plants was estimated by grinding samples and using a nitrate analyzer (Leco FPS 528; Leco, St. Joseph, MI) to calculate nitrogen as a proportion of dry weight (Bronson et al. 2001).

Each of the variables of interest, *A. gossypii*, *F. occindentalis*, and *B. tabaci* densities, was pooled over the 14-wk period, and these pooled sums were used in the statistical analyses. Pooling was performed to normalize the sampling distributions of each species, which were always non-normal during any single sampling period. Pooled samples were also more appropriate for examining relationships between insect densities and variables that did not change or were only measured once during the experiment, in particular, elevation and soil characteristics. To examine the effects of sampling area on correlation of the various independent and dependent variables, two sampling scales were used, whole field and block, along with two different grains (measurement distances), fine and coarse, at the whole field level. For both the whole field-fine grain level and block level, all subplots were included in the analyses so that sampling distance or grain was the same, with the main difference being that the whole field plot included measurements from all four blocks. For whole field-coarse grain analyses, only one of every four subplots was used so that the distance between samples was twice that of the fine grain samples. We only compared fine and coarse grain analyses at the whole field scale, not at the block, because at the block scale there would not be enough sample points to obtain reliable regressions.

Independent variables examined included plant height (cm), elevation (m), salinity (ds/m-electrical conductivity), pH 6/3 (3 June or early season), pH 8/5 (5 August or late season), predator density (per plant), whole plant moisture, soil nitrate concentration, proportion leaf nitrate, and proportions of clay, sand, and silt. For whole plant moisture, proportion leaf nitrate, and proportions of clay, sand, and silt, proportions were used in the statistical analyses, although percentages are given in tables. Pairwise correlation's between all independent variables were calculated at each scale and grain for determination of variables to remove from multiple regression models to prevent autocorrelation (pairwise command in JMP; SAS Institute, Cary, NC).

To assess the separate effects of each of the 12 different independent variables (listed in the previous paragraph) on *A. gossypii*, *F. occindentalis*, and *B. tabaci* densities, partial correlation matrices were calculated using the partial correlations command in JMP (SAS Institute). Each matrix was composed of each of the independent variables correlated with one of the dependent variables for the whole field at both the coarse grain and fine grain levels and for each of the blocks (fine grain).

To assess the overall affects of all 12 different independent variables and their two-way interactions (Table 1) on *A. gossypii, F. occindentalis,* and *B. tabaci* densities, forward stepwise regressions were performed using the fit model and stepwise commands in JMP (SAS Institute), with the decision for variables to be included in the model set at $\alpha = 0.1$. Separate multiple regressions were run for each of the dependent variables for the whole field at both the coarse grain and the fine grain level and once for each of the four blocks. Information from the autocorrelation data and from the correlation matrices were used to decide which of correlated independent variables to include and which to exclude from stepwise regression analyses.

Results

Pairwise Correlation's of Independent Variables. We found that pairs of several independent variables were significantly correlated and that the significance of these correlations was dependent on sampling scale and grain (Table 2). For this reason, to prevent autocorrelation in multiple regression analyses, one variable of each pair of correlated independent variables

Table 1. Autocorrelations (*r*) of independent variables used in stepwise multiple regressions for each of two sampling scales: whole field and blocks

	Whole field		Block (fine grain)			
	Fine grain	Coarse grain	1	2	3	4
Elevation × plant height	x	x	0.433	0.659	x	0.499
pH 6/3 × plant height	x	x	x	x	x	−0.417
pH 6/3 × elevation	x	0.436	x	x	x	−0.508
pH 6/3 × salinity	x	x	x	−0.477	x	x
Predator × plant height	x	x	0.499	x	x	x
Predator × pH 8/5	x	x	x	−0.529	x	x
Plant H_2O × elevation	0.236	x	x	x	x	x
Plant H_2O × pH 6/3	0.277	0.467	x	x	x	0.452
Plant H_2O × predator	x	0.412	x	x	x	x
Soil NO^{-3} × elevation	0.217	0.582	x	−0.496	0.417	x
Soil NO^{-3} × pH 6/3	0.269	x	x	x	x	−0.447
Soil NO^{-3} × predator	x	0.474	x	x	x	x
Soil NO^{-3} × plant H_2O	x	0.445	x	x	x	x
%Clay × elevation	−0.421	0.445	x	x	0.438	x
%Clay × predator	X	x	x	x	0.476	0.511
%Sand × elevation	−0.402	0.523	x	x	x	x
%Sand × leaf NO^{-3}	x	0.562	x	x	x	x
%Sand × %clay	−0.675	−0.670	−0.478	−0.562	0.551	−0.861
%Silt × elevation	X	x	0.505	x	x	x
%Silt × predator	X	x	x	x	−0.470	x
%Silt × plant H_2O	X	x	x	x	−0.533	x
%Silt × leaf NO^{-3}	X	0.449	x	x	x	
%Silt × %clay	X	x	x	−0.581	x	x
%Silt × %sand	−0.615	0.531	0.642	x	−0.641	−0.737

Only r^2 values for significant correlations ($\alpha < 0.05$) are listed; nonsignificant correlations were indicated with an x.

was excluded from all analyses at the particular scale and grain for which the variables were correlated.

***Aphis gossypii* Glover.** From the partial correlation matrices of the 12 independent variables and *A. gossypii* (Fig. 1), we found that no one variable was significantly correlated with *A. gossypii* density in all plots for each scale and grain, although plant moisture was positively correlated and early season pH (pH6/3, measured on 3 June) was negatively correlated with *A. gossypii* density in all plots. At the whole field scale, elevation was significantly and negatively correlated with *A. gossypii* density at both grains. At the whole field fine grain level, the variables significantly correlated with *A. gossypii* were elevation (−), pH 6/3 (−), pH 8/5 (−), and plant moisture (+) (Fig. 1A). At the whole field coarse grain level, the variables significantly correlated with *A. gossypii* were plant height (+), elevation (−), and sand (−) (Fig. 1B). At the block scale, no one variable was significantly correlated with *A. gossypii* density. Plant height (−), elevation (−), soil salinity (+), pH 8/5 (−), and leaf nitrate (+) were all significantly correlated with *A. gossypii* density in block 1 (Fig. 1C); plant moisture (+) was significantly correlated in block 2 (Fig. 1D); plant height (−), soil salinity (+), pH 6/3 (−), plant moisture (+), and clay (−) were all significantly cor-

Table 2. Means for all independent (predator densities, plant, soil, and landscape variables) and dependent (herbivore densities) variables used in stepwise multiple regressions for each of two sampling scales (whole field and block), and grains (fine and coarse)

	Whole field		Block (fine grain)			
	Fine grain	Coarse grain	1	2	3	4
Plant height (cm)	42.4 (1.1)	42.2 (1.9)	40.9 (1.3)	41.3 (1.3)	44.1 (2.8)	43.4 (2.6)
Elevation (m)	91.5 (0.2)	91.9 (0.3)	91.2 (0.2)	90.3 (0.2)	91.1 (0.2)	93.3 (0.2)
Salinity (d/Sm)	0.46 (0.01)	0.45 (0.03)	0.48 (0.03)	0.40 (0.02)	0.48 (0.02)	0.48 (0.02)
pH 6/3	7.46 (0.03)	7.51 (0.06)	7.33 (0.04)	7.42 (0.05)	7.55 (0.07)	7.56 (0.06)
pH 8/5	7.21 (0.02)	7.18 (0.04)	7.21 (0.04)	7.16 (0.04)	7.23 (0.03)	7.24 (0.03)
Predator	0.24 (0.02)	0.25 (0.05)	0.22 (0.05)	0.32 (0.06)	0.19 (0.04)	0.24 (0.05)
%Plant H_2O	63.5 (1.3)	65.2 (2.0)	63.9 (1.6)	59.5 (3.9)	62.1 (2.3)	67.9 (2.0)
%Soil NO^{-3}	2.83 (0.03)	2.80 (0.06)	2.96 (0.03)	2.84 (0.04)	2.90 (0.09)	2.61 (0.05)
%Leaf NO^{-3}	3.43 (0.02)	3.40 (0.03)	3.43 (0.05)	3.40 (0.04)	3.40 (0.03)	3.48 (0.06)
%Clay	18.5 (0.3)	18.5 (0.7)	19.4 (0.4)	16.8 (0.6)	17.7 (0.6)	20.0 (0.6)
%Sand	76.8 (0.4)	76.7 (0.8)	77.3 (0.5)	79.3 (0.5)	76.5 (0.8)	74.0 (0.8)
%Silt	4.7 (0.3)	4.8 (0.6)	3.3 (0.5)	3.9 (0.5)	5.8 (0.7)	6.0 (0.4)
Herbivore densities						
A. gossypii	150 (11)	138 (18)	170 (23)	138 (14)	147 (29)	147 (20)
F. occidentalis	14.9 (0.8)	15.4 (1.4)	15.3 (1.8)	18.4 (1.5)	15.0 (1.4)	10.9 (1.3)
B. tabaci	4.7 (0.3)	4.8 (0.6)	6.0 (0.69)	5.4 (0.7)	4.3 (0.6)	3.3 (0.5)

Numbers within parentheses are SEs. All insect species densities are means per leaf summed over the growing season.

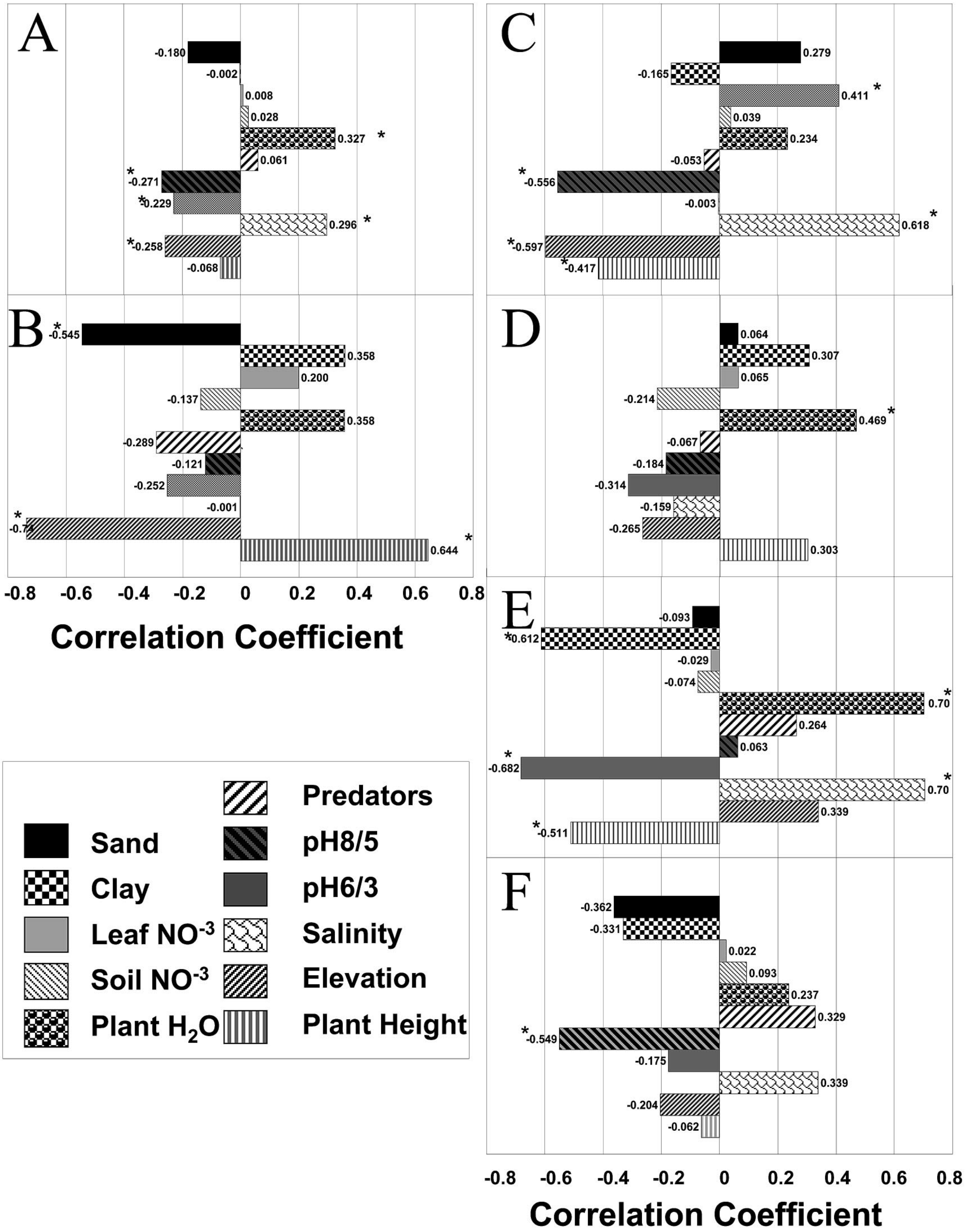

Fig. 1. Partial correlation coefficients of soil, plant, and landscape variables with *A. gossypii* densities for a whole cotton field with sampling at a fine and coarse (measurement distances twice as great as for fine) grain scale and for four blocks within the whole field sampled at the fine grain scale: (A) whole field-fine grain scale, (B) whole field-coarse grain scale, (C) block 1, (D) block 2, (E) block 3, and (F) block 4.

related in block 3 (Fig. 1E); and pH 8/5 (−) was significantly correlated in block 4 (Fig. 1F).

Stepwise regression of all uncorrelated variables on *A. gossypii* density at each scale and grain indicated that only plant moisture and soil nitrates were significant for all plots. However, there were differences in the signs and magnitude of these relationships. For plant moisture, the relationships were positive for all

Table 3. Results of stepwise regressions of several independent variables and their interactions on the mean proportion of *A. gossypii* density for two scales (whole field and block) and two grains (fine and coarse)

Variable	Whole field		Block (fine grain)			
	Fine grain	Coarse grain	1	2	3	4
Plant height	−	−		+	+	−
Elevation			−			
Salinity	+					+
pH 6/3		−	+	−	−	
pH 8/5	−		−	−	−	−
Predator	+		+			+
Plant H_2O	+	+	−	+	+	+
Plant H_2O × pH 6/3		+		+	+	
Plant H_2O × redator			+			+
Soil NO^{-3}	+	+	−	+	−	−
Soil NO^{-3} × plant height				+	−	
Soil NO^{-3} × plant H_2O				+	+	
Leaf NO^{-3}	+		−	−		−
Leaf NO^{-3} × plant height	+			−	−	
Leaf NO^{-3} × pH 6/3				−	−	
Leaf NO^{-3} × plant H_2O			−			−
Leaf NO^{-3} × soil NO^{-3}	+					+
%Clay	−	−	+		−	
%Clay × plant height	−	−			−	
%Clay × soil NO^{-3}	−				+	
%Sand				−		+
%Sand × plant height			−		−	
%Sand × plant H_2O				−		+
Adjusted R^2	0.31	0.77	0.55	1.0	1.0	1.0

All marked variables (positive or negative) were significant at $\alpha < 0.05$ and included in the overall model for which the R^2 results are given.

except block 1, which was negative, and for plant nitrates, the relationships were positive for the whole field at both grains and negative for all blocks except for block 2. Also, pH 8/5 was significant and negative in all fine grain plots (whole field and all four blocks). A number of other variables were also significant at each scale and grain, but the significance of both single variables and interactions varied greatly (Table 3). Also, R^2 values increased as scale decreased for fine grain measurements, with significant variables accounting for ≈31% of the variation in *A. gossypii* density at the whole field scale and 55, 100, 100, and 100% variation for each of the 4 blocks at the smaller scale (Table 3). Grain also affected R^2, with significant variables accounting for 77% of the variation in *A. gossypii* density at the whole field coarse grain level, much greater than for the fine grain level and intermediate compared with blocks.

***Frankliniella occidentalis* (Pergande).** As with *A. gossypii* (Fig. 2), we found that no one variable was significantly correlated with *F. occidentalis* density in all plots for each scale and grain, although soil nitrates were negatively correlated with *F. occidentalis* density at each scale and grain. At the whole field scale, only plant moisture was significant, but only at the fine grain scale, although it was negative at both scales. At the whole field scale, only plant moisture (−) was significantly correlated with *F. occidentalis* density at both the fine (Fig. 2A) and coarse grain scale (Fig. 2B). At the block scale, no variable was significantly correlated with *F. occidentalis* density. Soil salinity (−), predators (−), plant moisture (−), and clay (+) were significantly correlated with *F. occidentalis* density in block 1 (Fig. 2C); plant height (−) and soil salinity (+) were significantly correlated in block 2 (Fig. 2D); elevation (+), soil salinity (+), pH 8/5 (+), plant moisture (+), clay (−), and sand (−) were all significantly correlated in block 3 (Fig. 2E); and no variable was significantly correlated in block 4 (Fig. 2F).

Stepwise regression of all uncorrelated variables on *F. occidentalis* density at each scale and grain indicated that no variable was significant in all plots across scale or grain (Table 4). Also, no variable was significantly correlated with *F. occidentalis* density in all four blocks. A number of variables were significant for each plot at each scale and grain (Table 4), but the significance of both single variables and interactions varied greatly with scale and grain. Similar to *A. gossypii*, R^2 values increased as scale decreased for fine grain measurements, with significant variables accounting for ≈21% of the variation in *F. occidentalis* density at the whole field scale, and 29, 53, 75, and 85% variation for each of the 4 blocks at the smaller scale (Table 4). Grain also affected R^2, with significant variables accounting for 67% of the variation in *F. occidentalis* density at the whole field coarse grain level, much greater than for the fine grain level and intermediate compared with blocks.

***Bemisia tabaci* (Glenn.).** As with *A. gossypii* and *F. occidentalis* (Fig. 3), we found that no one variable was significantly correlated with *B. tabaci* density in all plots for each scale and grain, although soil salinity was positively correlated with *B. tabaci* density in all plots. At the whole field scale, salinity was significantly and positively correlated with *B. tabaci* density at both grains. At the whole field fine grain scale, the variables significantly correlated with *B. tabaci* density were elevation (−) and soil salinity (+) (Fig. 3A). At the whole field coarse grain scale, soil salinity (+), pH 6/3 (+), pH 8/5 (−), predators (+), soil nitrate (+), leaf nitrate (−), and clay (−) were all correlated with *B. tabaci* density (Fig. 3B). At the block scale, no variable was significantly correlated with *B. tabaci* density. No variable was significantly correlated with *B. tabaci* density in block 1 (Fig. 3C); soil salinity (+), pH 8/5 (+), predators (+), and leaf nitrates (+) were all correlated with *B. tabaci* density in block 2 (Fig. 3D); plant height (+) and pH 8/5 (−) were significantly correlated in block 3 (Fig. 3E); and salinity (+) and pH 6/3 (+) were significantly correlated in block 4 (Fig. 3F).

Similar to *F. occidentalis*, stepwise regression of all uncorrelated variables on *B. tabaci* density at each scale and grain indicated that no variable was significant in all plots across scale and grain (Table 5). However, salinity and plant height were positively (significantly) correlated with *B. tabaci* density in whole field coarse and fine grain plots. At the block level, no variable was significantly correlated with *B. tabaci* density in all blocks. A number of other vari-

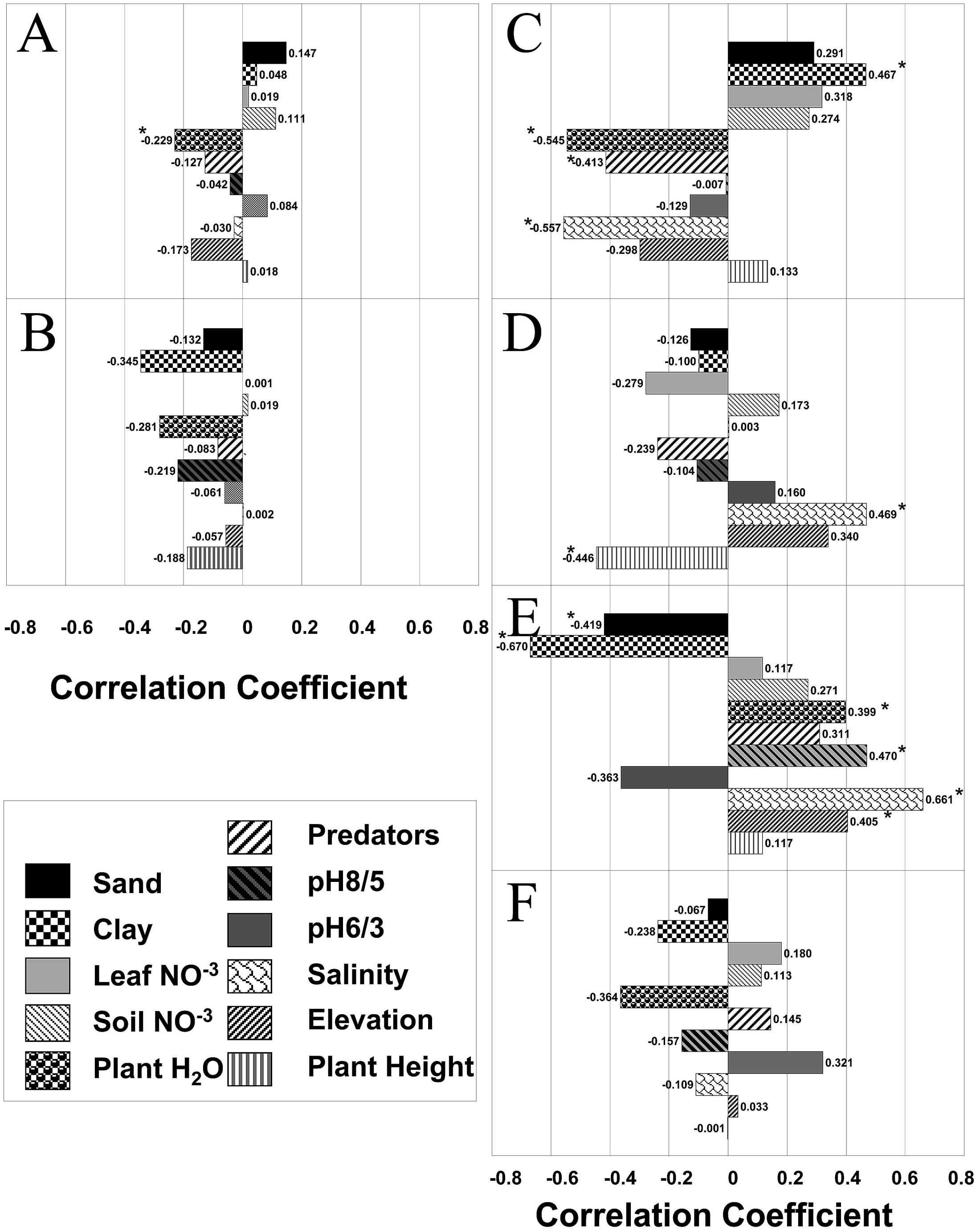

Fig. 2. Partial correlation coefficients of soil, plant, and landscape variables with *F. occidentalis* densities for a whole cotton field with sampling at a fine and coarse (measurement distances twice as great as for fine) grain scale and for four blocks within the whole field sampled at the fine grain scale: (A) whole field-fine grain scale, (B) whole field-coarse grain scale, (C) block 1, (D) block 2, (E) block 3, and (F) block 4.

ables were also significant for each plot at each scale and grains (Table 5), but the significance of both single variables and interactions varied greatly. Again, R^2 values increased as scale decreased for fine grain measurements, with significant variables accounting for ≈16% of the variation in *B. tabaci* density at the whole field scale and 100, 91, 43, and 68% variation for each of the 4 blocks at the smaller scale (Table 5).

Table 4. Results of stepwise regressions of several independent variables and their interactions on the mean proportion of *F. occidentalis* density for two scales (whole field and block) and two grains (fine and coarse)

Variable	Whole field		Block (fine grain)			
	Fine grain	Coarse grain	1	2	3	4
Plant height	–	+			+	–
Elevation			–			
Salinity			–	+	+	–
pH 8/5		–	–			+
Plant H_2O	–	–	+			–
Plant H_2O × pH 8/5		+	+			–
Soil NO^{-3}			+		+	+
Leaf NO^{-3}				–	–	
Leaf NO^{-3} × salinity				–	–	
%Sand	+		+			
%Silt	+	–		–		
%Silt × plant height	+	+				
Adjusted R^2	0.21	0.67	0.85	0.29	0.53	0.75

All marked variables (positive or negative) were significant at $\alpha < 0.05$ and included in the overall model for which the R^2 results are given.

Grain also affected R^2, with significant variables accounting for 46% of the variation in *F. occidentalis* density at the whole field coarse grain scale, greater than for the fine grain, and similar to the lowest block value.

Discussion

Our results indicated that several plant and soil characteristics were weakly to moderately correlated with sap-feeding insect densities in cotton. Our results also indicated that the direction and extent of these relationships were strongly related to both the herbivore species examined and to the scale and grain of the observations. Scale, as we use the term here, is the size of the area being sampled (whole field scale = 622 by 31 m and block scale = 154 by 31 m), whereas grain is the distance between sampling points (either 25 or 50 m in our study) (Obeysekera and Rutchey 1997). Both can affect the patterns or processes in soil or cotton plants in the field, and therefore, can also affect herbivore diversity or abundance (Funderburk et al. 1994, Qi and Wu 1996, Oline and Grant 2002). Because of the differences in variables affecting each insect species at each scale and grain examined in the current study, there was really no one characteristic that could be used to predict densities of the three herbivores. This was particularly true when we included interactions in the multiple regression models. For each insect species and for each scale and grain that we looked at, there was a suite of different significant interactions making it impossible to include any interactions in prediction models of herbivore density at different sampling scales or for different grains.

The most surprising results of our study were that the landscape and soil characteristics, elevation, salinity, and nitrate were the variables most consistently related to *A. gossypii* and *B. tabaci* densities. Plant characteristics such as height, moisture, and nitrates were less important, but did have some effect on each herbivore species. These results indicate that the most important field variables for use in predicting densities of these herbivores are certain soil and landscape characteristics, variables generally not examined by researchers (Wolfson 1980, Dale 1988, Lambert and Heatherley 1991, Funderburk et al. 1994). Even the insect species relationships with these variables, however, were affected by both the scale or size of the sampling area and the grain or distance between samples taken, as well as being affected by the other variables examined.

In this study, we found that salinity was positively correlated with *B. tabaci* density. A saline soil is one with an electrical conductivity >4 dS/m, and cotton yields are generally not affected until electrical conductivity reaches 9 dS/m (Hake et al. 1996). Studies linking soil salinity with insect abundance are lacking; however, extrapolation of plant-mediated effects of salinity on insects can be made from studies of the effects of salinity on plants and the few studies of plant-mediated salinity affects on herbivores of marsh plants. Salinity induces a number of chemical, physiological, and morphological plant changes that can affect herbivores (Dale 1988, Hwang and Morris 1994, Hester et al. 1996). These changes in the plant are either caused by a decrease in the osmotic potential at the root surface that decreases water availability or salinity has direct toxic effects (Terry and Waldron 1984). Increases in salinity and decreases in available moisture increase succulence (Rains 1972). Salt stress may cause water stress and a concentration of organic solutes (Hale and Orcutt 1987). In particular, leaves of salt stressed plants usually are higher in sugar concentration (Nieman and Clark 1976), a factor that is important to sap feeding insects such as aphids and whitefly.

Moon and Stilling (2002) found that increasing the salinity in a salt marsh decreased plant foliar nitrogen, but increased plant hopper densities within 1 mo of salt applications. Additionally, Bowdish and Stilling (1998) found that densities of the delphacid planthopper, *Prokelisia marginata* (Van Duzee), increased with additions of salt, fertilizer, or salt and fertilizer, despite that adding fertilizer increased plant nitrogen, whereas adding salt decreased plant nitrogen. In both of these cases, total foliar nitrogen was measured, but as Moon and Stilling (2002) point out, White (1984) proposed that stress would increase the mobilization of bound nitrogen, making unbound nitrogen more available to herbivores, and in neither study were the bound and unbound nitrogen measured separately. This may be the reason we were unable to detect foliar nitrogen affects on herbivore densities in the current study, although we did observe that soil salinity was negatively associated with herbivore densities.

Li et al. (2002) showed that site elevation and soil texture interacted with irrigation and nitrogen application rates to influence cotton yield. Li et al. (2001) also found that soils in lower elevation areas contained more water from water draining down from upslope areas, resulting in increased water and nutrient uptake

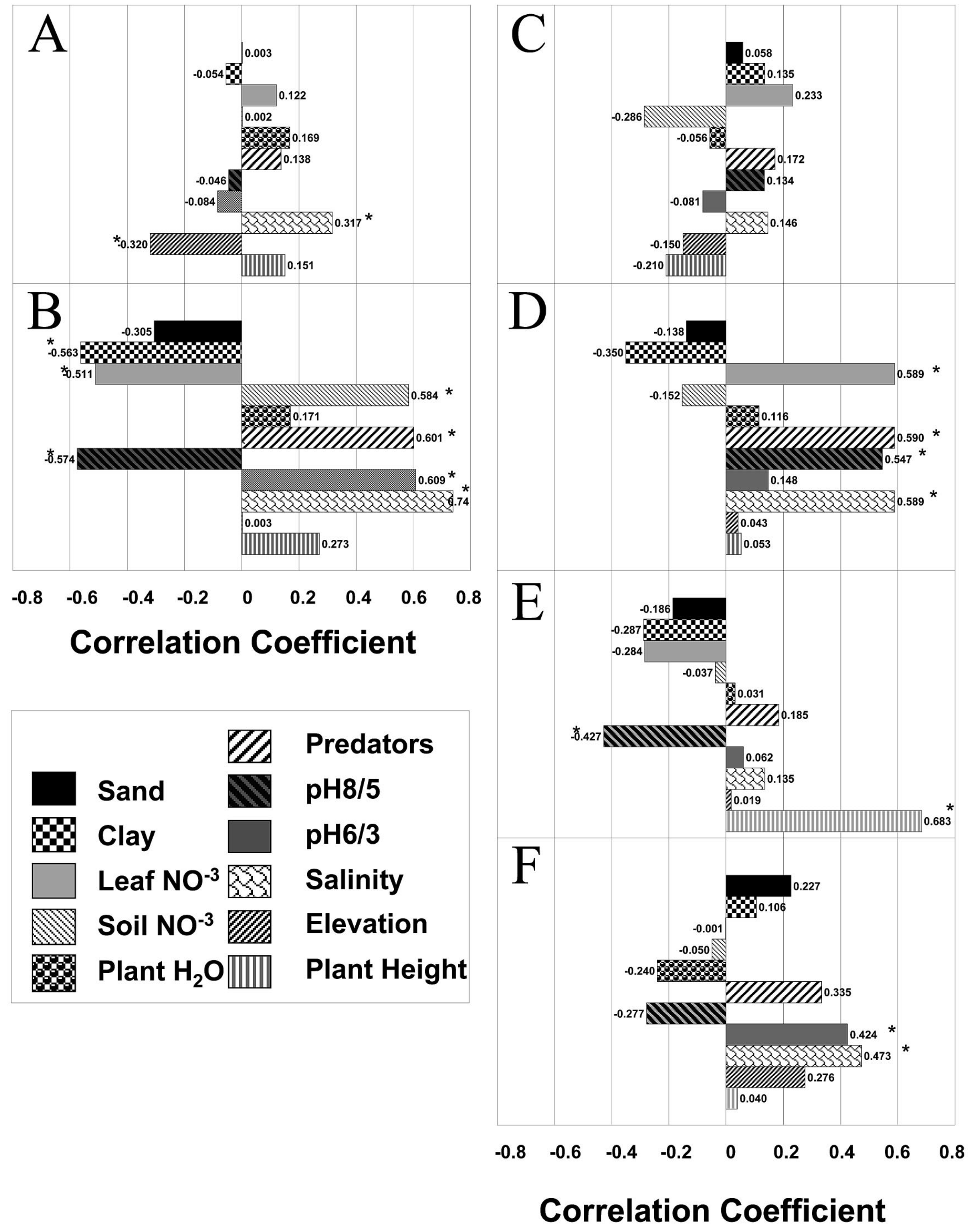

Fig. 3. Partial correlation coefficients of soil, plant, and landscape variables with *B. tabaci* densities for a whole cotton field with sampling at a fine and coarse (measurement distances twice as great as for fine) grain scale and for four blocks within the whole field sampled at the fine grain scale: (A) whole field-fine grain scale, (B) whole field-coarse grain scale, (C) fine grain scale block 1, (D) fine grain scale block 2, (E) fine grain scale block 3, and (F) fine grain scale block 4.

and higher yields. Elevation and soil texture may affect plants through water and nutrient availability (Clark 1982, Timlin et al. 1998). Therefore, decreasing elevation may increase plant health, increasing plant acceptability to some herbivores such as we found with *B. tabaci* in this study. Similar to our findings, Alonso

Table 5. Results of stepwise regressions of several independent variables and their interactions on the mean proportion of *B. tabaci* density for two scales (whole field and block) and two grains (fine and coarse)

Variable	Whole field		Block (fine grain)			
	Fine grain	Coarse grain	1	2	3	4
Plant height	+	+			+	−
Elevation	−		−	+		
Salinity	+	+	+	+		+
pH 8/5		+	−		−	−
pH 8/5 × plant height					−	+
pH 8/5 × salinity		−	+			−
Predator			+	+	+	−
Plant H_2O			+	+		
Soil NO^{-3}		+				
Leaf NO^{-3}	+		−	+		
Leaf NO^{-3} × salinity	+			+		
%Sand		−				
Adjusted R^2	0.16	0.46	1.0	0.91	0.43	0.68

All marked variables (positive or negative) were significant at $\alpha < 0.05$ and included in the overall model for which the R^2 results are given.

(1999) found a negative correlation between herbivory by *Yponomeuta mahalebella* Guenée on it host plant *Prunus mahaleb* L. and elevation, but their results were on much larger scale than examined here. McClure (1977) indicated that population success of a sale insect on eastern hemlock, *Tsuga canadensis* L. Carr., was influenced by the nutrient composition, texture, and moisture content of the soil.

Frankliniella occidentalis density was related to only biological factors, with plant moisture negatively correlated with *F. occidentalis* density in all plots. Wolfson (1980) described leaf-water content as important in larval development, but said it is often overlooked in host choice tests. Shorey (1964) showed that water content was important in oviposition choice by *Trichoplusia ni* Hübner females and implicated as important in studies of *Pieris rapae* L. by Benepal and Hall (1967) and Ives (1978). Increased water content may lead to decreased concentrations of nutrients, suggesting why *F. occidentalis* densities were negatively correlated with water content in this study. However, this does not explain why *A. gossypii* and *B. tabaci* densities were not related to plant water content, nor does it explain why herbivore densities were not related to leaf nitrates. One possible reason for the variation between herbivore species is that *F. occidentalis* feeds on the contents of cells, whereas the other two herbivores feed on phloem sap, which may differ in water and nutrient content from cells. Also, although nitrogen is often a limiting factor in the growth of most herbivores, other nutrients may have been more important during our study.

In conclusion, within-field soil characteristics may be more important as determinants of insect herbivore density than previously thought. Although it's likely that these characteristics were linked to plant characters that were not measured in this study, soil characters are much more constant than plant characters, making them more useful for predicting herbivore densities. Equally important was our finding that the relationship of each variable with a particular herbivore density was dependent on the scale and grain of the measurements. This leads us to the conclusion that both scale and grain are important in understanding the true importance of plant and soil characteristics to herbivore densities within cotton fields. Also, our findings indicate that insect herbivore samples need to be taken over a relatively large scale (≈2 ha as opposed to 0.5 ha) to more accurately predict the effects of plant, soil, and landscape characteristics on their densities. Finally, our findings, although limited to one season, suggest the possibility of using landscape and soil characteristics to define areas of a cotton field where sampling for pest control determinations may be concentrated.

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References Cited

Alonso, C. 1999. Variation in herbivory by *Yponomeuta mahalabella* on its only host plant *Prunus mahaleb* along an elevational gradient. Ecol. Entomol. 24: 371–379.

Alstad, D. N., G. F. Edmonds Jr., and L. H. Weinstein. 1982. The effect of air pollutants on insect populations. Annu. Rev. Entomol. 27: 369–384.

Benepal, P. S., and C. V. Hall. 1967. Biochemical composition of host plants of *Brassica oleracea var. capitata* (L.) as related to resistance of *Trichoplusia ni* Hubner and *Pieris rapae* Linne. Proc. Am. Soc. Hortic. Sci. 91: 325–330.

Bian, L., and S. J. Walsh. 1993. Scale dependencies of vegetation and topography in mountainous environment of Montana. Prof. Geog. 45: 1–11.

Bowdish, T. I., and P. Stilling. 1998. The influence of salt and nitrogen on herbivore abundance: direct and indirect effects. Oecologia (Berl.). 113: 400–405.

Bronson, K. F., A. B. Onken, J. W. Keeling, J. D. Booker, and H. A. Torbert. 2001. Nitrogen response in cotton as affected by tillage system and irrigation level. Soil Sci. Soc. Am. J. 65: 1153–1163.

Brosofske, K. D., J. Chen, T. R. Crow, and S. C. Saunders. 1999. Vegetation responses to landscape structure at multiple scales across a northern Wisconsin, USA, pines barren landscape. Plant Ecol. 143: 203–218.

Carrow, J. R., and R. E. Betts. 1973. Effects of different nitrogen fertilizers on balsam woolly aphid. Can. J. For. Res. 3: 122–139.

Chapin, S. F. 1991. Effects of multiple environmental stresses on nutrient availability and use, pp. 67–88. *In* H. A. Mooney, W. E. Winner, and E. J. Pell (eds.), Response of plants to multiple stresses. Academic, San Diego, CA.

Chew, F. S. 1977. Coevolution of pierid butterflies and their cruciferous foodplants. II. The distribution of eggs on potential foodplants. Evolution. 31: 568–579.

Clark R. B. 1982. Plant response to mineral element toxicity and deficiency, pp. 71–142. *In* M. N. Christiansen and C. F. Lewis (eds.), Breeding plants for less favorable environments. Wiley, New York.

Dale, D. 1988. Plant-mediated effects of soil mineral stresses on insects, pp. 35–110. *In* E. A. Heinrichs (ed.), Plant stress-insect interactions. Wiley, New York.

Dethier, V. G. 1959. Egg-laying habits of Lepidoptera in relation to available food. Can. Entomol. 91: 554–561.

Faria, M. L., and G. W. Fernandes. 2001. Vigour of a dioecious shrub and attack by a galling herbivore. Ecol. Entomol. 26: 37–45.

Funderburk, J. E., F. M. Rhoads, and I. D. Teare. 1994. Modifying soil nutrient level affects soybean insect predators. Agron. J. 86: 581–585.

Gee, G. W., and J. W. Bauder. 1986. Particle-size analysis, pp. 383–411. *In* A. Klute (ed.), Methods of soil analysis, part 1, 2nd ed. American Society of Agronomics and Soil Science Society of America, Madison, WI.

Hake, S. J., K. D. Hake, and T. A. Kerby. 1996. Postharvest-fall, pp. 1–5. *In* S. J. Hake, T. A. Kerby, and K. D. Hake (eds.), Cotton production manual. University of California Division of Agriculture and Natural Resources, Oakland, CA.

Hale, M. G., and D. M. Orcutt. 1987. The physiology of plants under stress. A Wiley Interscience Publication. Wiley and Sons Inc., New York.

Halvorson, G. A., and E. C. Doll. 1991. Topographic effects on spring wheat yields and water use. Soil Sci. Soc. Am. J. 55: 1680–1685.

Hester, H. W., I. A. Mendelssohn, and K. L. McKee. 1996. Intraspecific variation in salt tolerance and morphology in the coastal grass *Spartina patens* (Poaceae). Am. J. Bot. 83: 1521–1527.

Hodkinson, I. D., J. M. Bird, J. K. Hill, and R. Baxter. 2001. Host plant growth characteristics as determinants of abundance and phenology in jumping plant-lice on downy willow. Ecol. Entomol. 26: 376–387.

Hwang, Y. H., and J. T. Morris. 1994. Whole-plant gas exchange responses of *Spartina alterniflora* (Poaceae) to a range of constant and transient salinities. Am. J. Bot. 81: 659–665.

Ives, P. M. 1978. How discriminating are cabbage butterflies? Aust. J. Ecol. 3: 261–276.

Joyce, R.J.V. 1958. Effect on the cotton plant in the Sudan Gezira of certain leaf-feeding pests. Nature (Lond.). 182: 1463–1464.

Kotilar, N. B. 1996. Scale dependency and the expression of hierarchical structure in *Delphinium* patches. Vegatation. 127: 117–128.

Lambert, L., and L. G. Heatherly. 1991. Soil water potential: effects on soybean looper feeding on soybean leaves. Crop. Sci. 31: 1625–1628.

Lascano, R. J. 2000. A general system to measure and calculate daily crop water use. Agron. J. 92: 821–832.

Li, H., R. J. Lascano, J. Booker, L. T. Wilson, and K. F. Bronson. 2001. Cotton lint yield variability in a heterogeneous soil at a landscape scale. Soil Till. Res. 58: 245–258.

Li, H., R. J. Lascano, J. Booker, L. T. Wilson, K. F. Bronson, and E. Segarra. 2002. State-space description of field heterogeneity: water and nitrogen use in cotton. Soil Sci. Soc. Am. J. 66: 585–595.

Mattson, W. J., and N. D. Addy. 1975. Phytophagous insects as regulators of forest primary production. Science. 190: 515–522.

McClure, M. S. 1977. Dispersal of the scale *Fiorinia externa* (Diaspididae) and effects of edaphic factors on its establishment on hemlock. Environ. Entomol. 6: 539–544.

McNeill, S. 1971. The energetics of a population of *Leptopterna dolabrata* (Heteroptera: Miridae). J. Anim. Ecol. 40: 127–140.

McNeill, S., and T.R.E. Southwood. 1978. The role of nitrogen in the development of insect/plant relationships, pp. 77–98. *In* J. B. Harborne and H. F. van Emden (eds.), Biochemical aspects of insect/plant interactions. Academic, New York.

Mitchell, R. G., and H. G. Paul. 1974. Field fertilization of Douglas fir and its effect on *Adelgis cooleyi* populations. Environ. Entomol. 3: 501–504.

Moon, D. C., and P. Stilling. 2002. Top-down, bottom-up, or side to side? Within-trophic-level interactions modify trophic dynamics of a salt marsh herbivore. Oikos. 98: 480–490.

Munns, R., H. Greenway, and G. O. Kirst. 1982. Halotolerant eukaryotes, pp. 55–139. *In* E. L. Lange, P. S. Nobel, C. B. Osmond, and H. Ziegler (eds.), Encyclopedia of plant physiology, new series, vol. 12C. Springer, Berlin, Germany.

Nieman, R. H., and R. A. Clark. 1976. Interactive effects of salinity and phosphorus nutrition on the concentrations of phosphate and phosphate esters in mature photosynthesizing corn leaves. Plant Physiol. 57: 157–161.

Obeysekera, J., and K. Rutchey. 1997. Selection of scale for Everglades landscape models. Landscape Ecol. 12: 7–18.

Oline, D. K., and M. C. Grant. 2002. Scaling patterms and soil properties: an empirical analyses. Landscape Ecol. 17: 1–14.

Pedigo, L. P. 1989. Entomology and pest management. Macmillan Publishing, New York.

Qi, Y., and J. G. Wu. 1996. Effects of changing spatial resolution on the results of landscape pattern analysis using spatial autocorrelation indices. Landscape Ecol. 11: 39–49.

Rains, D. W. 1972. Salt transport in plants in relation to salinity. Annu. Rev. Plant Physiol. 23: 367–388.

Rhoades, D. F. 1979. Evolution of plant chemical defenses against herbivores, pp. 3–54. *In* G. H. Rosenthal and D. H. Janzen (eds.), Herbivores: their interaction with secondary plant metabolites. Academic, New York.

Rodriguez-Iturbe, I., G. K. Vogel, and R. Rigon. 1995. On the spatial organization of soil moisture fields. Geophys. Res. Lett. 22: 2757–2760.

Scriber, J. M. 1984. Nitrogen nutrition in plants and insect invasion, pp. 441–460. *In* R. D. Hauck (ed.), Nitrogen in crop production. American Society of Agronomics, Madison, WI.

Sharma, M. L. 1970. Responses of phytophagous insects to treatments of nitrogen, potassium, and phosphorus applied to plants (general review). Ann. Soc. Entomol. Que. 15: 88–95.

Shorey, H. H. 1964. The biology of *Trichoplusia ni* (Lepidoptera: Noctuidae). III. Response to the oviposition substrate. Ann. Entomol. Soc. Am. 57: 165–169.

Smirnoff, W. A., and B. Bernier. 1973. Increased mortality of the Swaine jack-pine sawfly, and foliar nitrogen concentrations after urea-fertilization. Can. J. For. Res. 3: 112–121.

Southwood, T.R.E. 1972. The insect/plant relationship-an evolutionary perspective, pp. 3–30. *In* H. F. van Emden (ed.), Insect/plant relationships. Symposia of the Royal Entomological Society of London. Blackwell Scientific, Oxford, UK.

Tabashnik, B. E. 1982. Responses of pest and non-pest *Colias* butterfly larvae to interspecific variation in leaf nitrogen and water content. Oecologia (Berl.). 55: 389–394.

Terry, N., and L. J. Waldron. 1984. Salinity, photosynthesis, and leaf growth. Calif. Agric. 38: 38–39.

Timlin, D. J., Y. Pachepsky, V. A. Snyder, and R. B. Bryant. 1998. Spatial and temporal variability of corn grain yield on a hillslope. Soil Sci. Soc. Am. J. 62: 764–773.

Treshow, M. 1970. Environment and plant response. McGraw-Hill, New York.

van Emden, H. F., V. F. Eastop, R. D. Hughes, and M. J. Way. 1969. The ecology of *Myzus persicae.* Annu. Rev. Entomol. 14: 197–270.

Western, A. W., and G. Bloschl. 1999. On the spatial scaling of soil moisture. J. Hydrol. 217: 203–224.

White, T.C.R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia (Berl.). 63: 90–105.

Wolfson, J. L. 1980. Oviposition response of *Pieris rapae* to environmentally induced variation in *Brassica nigra.* Entomol. Exp. Appl. 27: 223–232.

Yu, M., E. Segarra, H. Li, R. J. Lascano, C. Chilcutt, L.T. Wilson, K. Bronson, and S. Searcy. 2000. The economics of precision agricultural practices in cotton production, pp. 369–374. *In* P. Dugger and D. A. Richter (eds.), Proceedings of the 2000 Beltwide Cotton Conference. National Cotton Council, Memphis, TN.

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